Effect of Plant Growth Regulator Paclobutrazol and Fertilization on Paper Birch and Austrian Pine Resistance to Folivores

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Abstract

Plant defense theory predicts that environmental factors that limit growth of plants more than their rate of photosynthesis should increase secondary metabolism and insect resistance. Applications of the plant growth regulator paclobutrazol slowed the growth of paper birch and Austrian pine with no effect on photosynthesis. In response, foliar concentrations of condensed tannins in birch increased as predicted, but with little effect on insect resistance. Growth and survival of gypsy moth, and forest tent caterpillar were not affected over the three year study period, and growth of whitemarked tussock moth larvae was reduced only slightly in one year. Contrary to the predictions, pine monoterpene concentrations were not affected by paclobutrazol and increased in response to fertilization. Nevertheless none of the treatments affected pine resistance to the European pine sawfly. Fertilization had no effects on tree growth, possibly due to high background levels of soil fertility, and decreased birch resistance to gypsy moth during the second year of study, but otherwise had no effect on insect performance. Although paclobutrazol decreased tree growth as expected, results provide little evidence to support claims that it can be used as a tool to enhance insect resistance.

Introduction

Numerous studies have demonstrated that increased growth rate of trees is often associated with decreased insect resistance (Herms and Mattson 1997; Herms 2002). This has been attributed to internal allocation tradeoffs in their carbon budget (Herms and Mattson 1992; Herms 2002). For example, fertilization increases growth rate because trees are stimulated to allocate a greater proportion of their carbon to production of new leaf area. However, root growth is proportionally decreased, as are concentrations of storage and defensive compounds (e.g. phenolics and other secondary metabolites) (Herms and Mattson 1997; Herms 2002). Conversely, studies have shown that trees in less fertile soils have higher root:shoot ratios, while maintaining high rates of photosynthesis and a strong energy budget even when growing slowly. As a result, these nutrient "stressed" plants often accumulate higher concentrations of defensive compounds and storage reserves, and are more resistant to insects (Herms and Mattson 1997; Herms 2002).

Paclobutrazol, by inhibiting gibberellin biosynthesis, may slow growth (Coolbaugh and Hamilton 1976) while maintaining photosynthetic rates (e.g. Wieland and Wample 1985). Since gibberellins share a biosynthetic pathway with secondary metabolites (Hanover 1975), and paclobutrazol inhibits its synthesis further in the chain of reactions (Coolbaugh and Hamilton 1976), it is possible to predict an increase in available photosynthates to be allocated to the production of secondary metabolites. Hence, paclobutrazol may increase secondary metabolism and insect resistance of trees through effects on resource allocation patterns similar to those caused by nutrient limitation.

Objective

- Quantify the effects of paclobutrazol and fertilization, separately and in combination, on the resource allocation (e.g. growth, photosynthesis, and foliar chemistry), and insect resistance of paper birch (*Betula papyrifera*) and Austrian Pine (*Pinus nigra*).

Research Methods

The study was conducted in 48 field plots (each $4m^2$ in area) designed to isolate the soil environment of individual trees. A single paper birch was planted in each plot on 20 September 2000, and a single Austrian pine was added to each plot on 12 September 2002. The experiment was designed as a randomized complete block, with four treatments: (1) untreated control, (2) paclobutrazol, (3) fertilized, and (4) paclobutrazol + fertilizer. There are 12 replicate trees per treatment, with each treatment combination replicated four times in each of three blocks.

Figure 1. Design and construction of test plots.

Paper birch trees were fertilized with half the recommended annual rate applied just after bud break in the spring, and the other half prior to leaf drop in late summer or early fall. Paclobutrazol was applied on 19 September 2003 to both paper birch and Austrian pine, according to labeled rates and protocols.

For paper birch we quantified growth, photosynthetic rate, and foliar concentrations of nitrogen and tannins. For pine, we quantified growth, as well as foliar nitrogen, phenolic, and monoterpene concentrations. Effects on birch resistance to gypsy moth (*Lymantria dispar*), forest tent caterpillar (*Malacosoma disstria*), and whitemarked tussock moth (*Orgyia leucostigma*), as well as resistance of Austrian pine to European pine sawfly (*Neodiprion sertifer*), were quantified in laboratory bioassays utilizing foliage from each experimental tree.

Results

Tree Growth. During 2003, paclobutrazol decreased the height and trunk diameter growth of both paper birch and Austrian pine, with fertilization having no effect. The growth-inhibiting response of Paclobutrazol was observed in the fertilized, as well as non-fertilized plots (no significant Paclobutrazol * fertilization interaction) (Tables 1 and 2). This effect persisted in Austrian pine until 2005 but not in paper birch.

Table 1. Paper birch growth

Treatment	Paper birch: Diameter growth rate (mm year^{-1}) 2003	2004	2005	Height growth rate (cm year^{-1}) 2003	2004	2005
Paclobutrazol	12.0 (2.5) b	6.2 (1.7) a	4.7 (1.1) a	72.8 (15.7) ac	58.6 (11.2) a	14.3 (4.3) a
Fertilized	21.8 (2.2) a	10.3 (1.4) a	3.0 (1.0) a	116.8 (18.5) a	77.2 (13.3) a	15.4 (5.0) a
Fertilized + Paclobutrazol	11.0 (3.3) b	8.9 (2.2) a	4.0 (1.5) a	52.2 (23.5) bc	44.5 (16.9) a	13.1 (6.4) a
Control	19.6 (2.0) a	7.8 (1.3) a	4.0 (0.9) a	90.2 (13.8) ab	57.6 (9.9) a	17.3 (3.8) a

Results of repeated measurements analysis in SAS. Effect on diameter growth: Paclobutrazol : 2003: p=0.0016; 2004: p=0.3576; 2005: p=0.4403, Fert: N/S, Paclobutrazol x Fertilized: N/S. Effect on height growth: Paclobutrazol : 2003: p=0.0232; 2004: p=0.1890; 2005: p=0.5546. Fert: N/S Paclobutrazol x Fertilized: N/S. Values followed by the same letter in a column do not differ statistically (p≥0.05).

Table 2. Austrian pine growth

Treatment	Austrian pine: Diameter growth rate (mm year^{-1}) 2003	2004	2005	Height growth rate (cm year^{-1}) 2003	2004	2005
Paclobutrazol	4.5 (0.6) ab	4.3 (0.9) b	5.4 (1.1) ab	20.3 (2.5) ab	7.2 (2.0) b	11.0 (2.8) b
Fertilized	5.6 (0.6) a	7.5 (0.9) a	7.4 (1.1) a	26.5 (2.5) a	17.2 (2.0) a	20.7 (2.8) a
Fertilized + Paclobutrazol	3.4 (0.6) b	5.1 (0.9) ab	2.5 (1.1) b	16.2 (2.5) b	4.6 (2.0) b	8.2 (2.8) b
Control	6.2 (0.6) a	6.2 (0.9) ab	7.6 (1.1) a	26.7 (2.5) a	17.5 (2.0) a	22.9 (2.8) a

Results of repeated measurements analysis in SAS. Effect on diameter growth: Paclobutrazol : 2003: p=0.0019; 2004: p=0.0265; 2005: p=0.0026, Fert: N/S, Paclobutrazol x Fertilized: N/S. Effect on height growth: Paclobutrazol : 2003: p=0.0016; 2004: p<0.0001; 2005: p<0.0001, Fert: N/S, Paclobutrazol x Fertilized: N/S. Values followed by the same letter in a column do not differ statistically (p≥0.05).

Photosynthesis. Paclobutrazol had no effect on net photosynthesis rate of paper birch and Austrian pine, which remained high in treated and untreated trees on the first two years of study (Table 3). However, in 2005 photosynthesis showed treatments effect.

Table 3. Treatments effect on photosynthetic rate (μmol CO_2 m^{-2}sec^{-1}). Figure shows pooled values of single measurements within a year.

Treatments	Paper birch 2003	2004	2005	Austrian pine 2004	2005
Paclobutrazol	14.10 (0.98) a	7.00 (1.06) a	13.32 (0.99) a	7.39 (0.93) a	6.53 (0.68) a
Fertilized	15.33 (0.98) a	8.06 (1.24) a	7.42 (1.29) b	9.15 (0.92) a	2.48 (0.67) b
Paclobutrazol + Fertilized	12.79 (0.98) a	8.88 (1.47) a	13.52 (1.72) a	6.69 (0.97) a	3.29 (0.67) b
Control	15.12 (1.02) a	7.69 (0.95) a	11.92 (0.95) a	6.97 (0.94) a	3.23 (0.67) b

PROC GLM (SAS). Standard error shown in parenthesis. Values followed by the same letter in a column do not differ statistically (p≥0.05).

Foliar Chemistry. Tannins concentration of birch foliage showed a significant increase in the paclobutrazol treated trees, on 2003 (Fig. 2). In Austrian pine, total monoterpenes increased as a result of the fertilization treatment (Fig. 3). Analysis of foliar nitrogen and tannins for the other years are not yet complete.

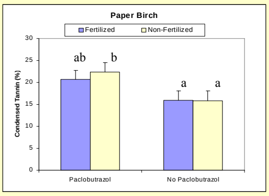

Figure 2. Paper birch tannins (%)

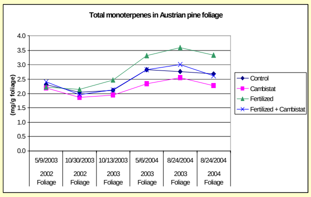

Figure 3. Austrian pine total monoterpenes

Insect Resistance. Paclobutrazol had no effect on paper birch resistance to gypsy moth or forest tent caterpillar, or Austrian pine resistance to European pine sawfly, as indicated by larval growth in laboratory bioassays conducted in May. Only a slight effect was observed during 2004, when birch resistance to gypsy moth decreased after fertilization, and to whitemarked tussock moth larvae in the paclobutrazol treated trees (Table 4).

Table 4. Treatments effect on insect growth (mg / 7day bioassay)

Treatments	Gypsy moth 2003	2004	2005	Forest tent caterpillar 2003	2004	Whitemarked tussock moth 2004	2005	European pine sawfly 2003	2004	2005
Paclobutrazol	70.19 (7.1) a	28.15 (4.0) b	13.45 (1.2) a	10.13 (1.5) a	2.45 (2.4) a	22.42 (1.7) a	16.72 (1.3) a	60.75 (2.7) a	104.37 (6.7) a	69.01 (3.5) a
Fertilized	67.65 (6.7) a	45.74 (4.1) a	13.78 (1.6) a	12.29 (1.5) a	6.56 (1.9) a	25.12 (1.9) ab	19.99 (1.8) a	65.10 (2.8) a	100.54 (6.7) a	58.67 (3.5) a
Paclobutrazol + Fertilized	68.60 (7.1) a	30.96 (5.4) b	14.51 (2.2) a	10.43 (1.6) a	4.12 (3.2) a	22.94 (2.6) ab	14.45 (2.0) a	65.36 (2.7) a	104.73 (6.7) a	64.83 (3.5) a
Control	67.09 (7.1) a	31.25 (3.8) b	13.45 (1.2) a	11.42 (1.6) a	1.63 (1.9) a	28.35 (1.6) b	16.87 (1.3) a	66.18 (2.7) a	105.75 (6.7) a	64.02 (3.5) a

PROC GLM (SAS). Standard error shown in parenthesis. Values followed by the same letter in a column do not differ statistically (p≥0.05).

Discussion

The expected effect of paclobutrazol was more evident during 2004 with decreased growth of both paper birch and Austrian pine, and without affecting photosynthetic rates. Plant allocation theory predicts that when growth is decreased with no accompanying effect on photosynthesis, then the availability of carbon to support other processes, such production of secondary metabolites and root growth, should increase, thereby increasing insect resistance (Herms and Mattson 1992,1997; Herms 2002). Consistently, paclobutrazol increased paper birch secondary metabolites (i.e. tannins), however it did not affect Austrian pine monoterpenes. Nevertheless, we observed no effect of paclobutrazol on birch resistance to gypsy moth and forest tent caterpillar, or resistance of Austrian pine to European pine sawfly. These results clearly indicated that paclobutrazol had no effect on tree resistance to insect folivores.

Surprisingly, fertilization had no effect on tree growth or insect resistance, perhaps due to high background fertility of the native soil, and / or because trees had acclimated to the fertility treatment. Interestingly, pine monoterpenes increased in the fertilized treatment suggesting the need for further research in this area.

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